

## 3. THE ECHOLOCATING ROLE OF EYES IN INSECTIVOROUS BATS

(With one plate)

The power of flight and ability to echolocate prey are responsible for the tremendous evolutionary success of bats. They skilfully navigate in pitch darkness over hill and dale, dextrously hunting for insects within brambles, thicket and bushes. D.R. Griffin coined the term 'echolocation' in 1944, to describe the method of self-information in which one organ emits a sound signal (the sonar apparatus) and another organ of the same animal receives it (radar mechanism). There are two suborders of bats: 1) the echolocating Microchiroptera and 2) the fruit and flower-visiting Megachiroptera or flying foxes of the Old World. Echolocating bats not only 'locate' a target, but also analyze its features; for example they distinguish prey from non-prey, and smooth from rough surfaces for landing. Since the term echolocation does not describe the full capacity of this acoustic information system, Neuweiler (1990) suggested the term 'audification' which is analogous to visualization.

The power of echolocation has conferred such advantages and glamour to microchiropteran bats, that extensive work has been done on this aspect. But surprisingly little is known about the precise use of their eyes in vision and prey capture. The only reference that Altringham (1996) makes to the function of vision in prey capture is that of Bell (1985) who discovered that the Californian leaf-nosed bat *Macrotus californicus*, a gleaner, used prey-generated sound and low intensity echolocation in localizing its prey. Under laboratory conditions, when the illumination was matched to bright moonlight, the bats located their prey by echolocation in only one third of the time "relying on vision for the remainder in the absence of prey movement and sound" (Altringham 1996). Larger carnivores such as the Australian ghost bat *Macroderma gigas*, the

Indian false vampire *Megaderma lyra* and *Cardioderma cor*, also have relatively large eyes, compared to exclusive insect feeders such as *Hipposideros speoris* and *H. bicolor*. There are, of course, many cues that hearing in microchiropteran bats is much more efficient than vision. One convincing morphological cue is that the auditory regions of the brain of insect eating bats are disproportionately larger than the optic regions, and are apparently specialized to receive, process, store, and retrieve information about the environment from soft echoes.

We have investigated the foraging strategies, 'best hearing frequencies' (BHF), and echolocation of eight species of insectivorous bats of Madurai (9° 58' N; 78° 10' E) (Neuweiler 1984; Neuweiler *et al.*, 1984; Habersetzer and Marimuthu 1986; Link *et al.*, 1986; Neuweiler *et al.*, 1988) *Tadarida aegyptiaca*, *Taphozous kachhensis*, *Taphozous melanopogon*, *Rhinopoma hardwickei*, *Pipistrellus mimus*, *Pipistrellus domeri*, *Hipposideros speoris* and *Hipposideros bicolor*. We have not conducted specific experiments on the role of eyes in flight; landing or prey captures in any of the species of bats we studied. Extensive data on the biology, chronobiology, (Subbaraj and Chandrashekar 1978; Marimuthu *et al.*, 1978) behaviour (Chandrashekar and Marimuthu 1987; Radhamani *et al.*, 1990), and ecology of *Hipposideros speoris*, *Taphozous melanopogon*, *Taphozous kachhensis*, and *Rhinopoma hardwickei* have been published. *Taphozous kachhensis* and *Hipposideros speoris* do perceive colours (Sripathi 1982, Joshi and Chandrashekar 1985) and so do four other species of microchiropteran bats (Hope and Bhatnagar 1979a, 1979b). The Madurai bats forage as efficiently on new moon nights and during a lunar eclipse as they do on full moon

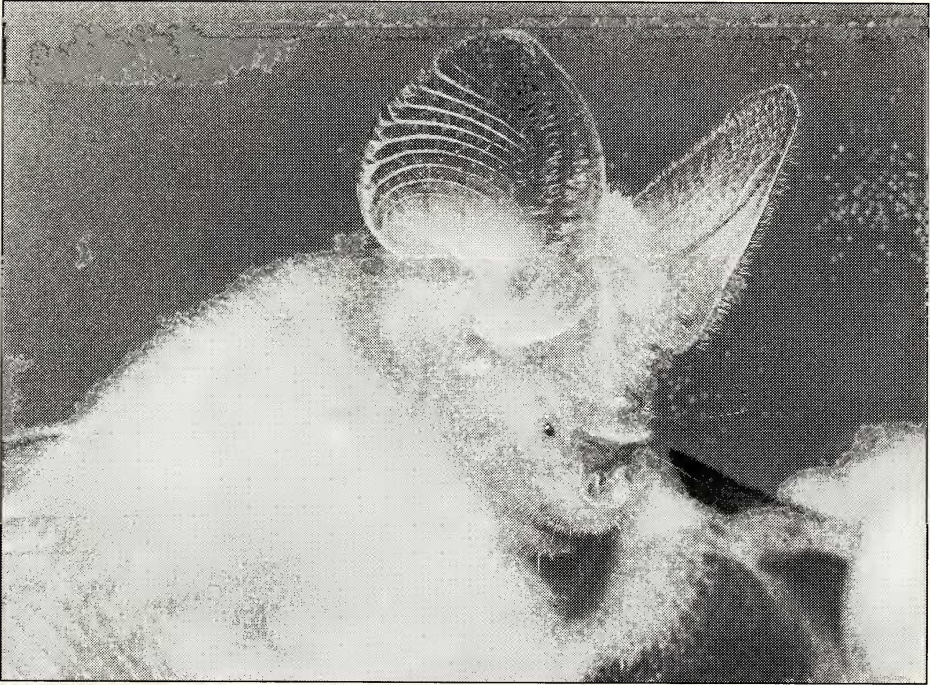


Fig. 1: A male adult *Hipposideros bicolor* (Note the very small eyes. This bat emits ultrasonics of a frequency of 155 kHz pure tone for echolocation and can hunt for insects in bramble and thicket.)



nights (Usman *et al.* 1981).

In field ethological studies on foraging in bats, it is difficult to create conditions of absolute darkness, as there is some light even on new moon nights. In fact, in our experiments on foraging by microchiropterans, the bats were attracted to insects that swarmed around an artificial (petromax) light source in the open, enabling bat counts. Which is why it becomes difficult to rule out with utmost certainty the possibility of participation of vision in prey capture. However, Marimuthu and Chandrashekar (unpublished) demonstrated that *Hipposideros speoris* could catch prey in an absolutely dark cave. The two species of hipposiderid bats which inhabit adjacent caves in Madurai in the Samanar Hills complex have the smallest eyes among the insectivorous bats of Madurai (Plate 1, Fig. 1), which interestingly emit the highest frequency of ultrasonic pulses. *H. speoris* emits pure tone of *ca* 132 kHz and *H. bicolor* of 155 kHz.

The account that follows describes a chance discovery, which is nevertheless valuable. G. Marimuthu was feeding bats held captive in activity cages (Marimuthu *et al.* 1978) inside a natural cave, 40 m from the cave mouth. The cave was absolutely dark at this place, hence he used a battery-operated torch, tied to the head, with a 'safe' red light of more than 610 nm. He was holding a live cockroach with a pair of forceps (from which the elytra, wings, cuticle and innards had been removed) when he had turned the torch off. Suddenly, he felt a jerk on his hand. Surprised, he switched on the torch to find the cockroach missing. On searching, he found a bat hanging from the ceiling of the cave chewing up the snatched cockroach. The free-flying bat had wrenched the wriggling cockroach off the forceps. This prey capture in darkness was obviously accomplished solely by means of echolocation in which *H. speoris* employs CF/FM signals of 5-10 msec of pure tone of *ca* 132 kHz terminated by a brief FM sweep (Neuweiler *et al.*, 1984).

Reverting to the role of the eyes,

insectivorous bats like *Hipposideros speoris* and *Rhinopoma hardwickei*, are known to 'sample light' 10-15 minutes prior to synchronized exodus, which coincides with sunset in Madurai (Marimuthu *et al.* 1981). When the twilight intensity falls below 0.3 lux (which is roughly the intensity of moonlight) the bats fly out. In adult mammals, the retinal photoreceptors are the only known route for light perception, and therefore blinding in a squirrel *Funambulus palmarum* and the mouse *Mus booduga*, resulted in free-running circadian rhythms (Navaneethakannan and Kumaraswamy, 1987). We have further shown that the circadian rhythms in the activity of *Hipposideros speoris* entrains to daylight of intensities which are 5 to 30% of starlight (0.002 lux) for *ca* 90 min every 24 hrs (Joshi and Chandrashekar 1982). In laboratory experiments with *H. speoris* we also demonstrated that brief flashes of light of 0.5 msec shifted the circadian rhythm as a function of phase (Joshi and Chandrashekar 1984).

On the basis of our findings, we conclude that the eyes of insectivorous bats such as *Hipposideros speoris* may not be very efficient in prey capture as they are small. The recurrent 'sampled' light pulses at the cave mouth, of a few minutes, that the bats are exposed to every 24 hrs, entrain their biological clocks. We further propose that it is not unlikely that the eyes play a crucial role as photoreceptors in this circadian entrainment.

#### ACKNOWLEDGEMENTS

I thank G. Marimuthu for help in performing the arduous experiments inside a natural cave in Keela Kuyil Kudi rock complex.

June 5, 2000 M. K. CHANDRASHEKARAN  
*Evolutionary and Organismal Biology Unit,  
 Jawaharlal Nehru Centre for Advanced  
 Scientific Research, P.O. Box 6436, Jakkur,  
 Bangalore 560 064, Karnataka, India.*

## REFERENCES

- ALTRINGHAM, J.D. (1996): Bats: Biology and Behaviour. Oxford University Press. Oxford, New York, Tokyo. Pp. 253.
- BELL, G.P. (1985): The sensory basis of prey location by the California leaf-nosed bat, *Macrotus californicus*. (Chiroptera: Phyllostomatidae). *Behav. Ecol. Sociobiol.* 16: 343-347.
- CHANDRASHEKARAN, M.K. & G. MARIMUTHU (1987): Sighting of a colony of the Indian false vampire bat, *Megaderma lyra*. *Bat Research News.* 26: 12.
- HABERSETZER, J. & G. MARIMUTHU (1986): Ontogeny of sounds in the echolocating bat *Hipposideros speoris*. *J. Comp. Physiol. A* 158: 247-257.
- HOPE, G.M. & K.P. BHATNAGAR (1979a): Electrical response of bat retina to spectral stimulation: comparison of four microchiropteran species. *Experientia* 35: 1189-1191.
- HOPE, G.M. & K.P. BHATNAGAR (1979b): Effect of light adaptation on electrical responses of the retina of four species of bats. *Experientia* 35: 1191-1193.
- JOSHI, D. & M.K. CHANDRASHEKARAN (1982): Daylight dimmer than starlight entrains the circadian rhythm of a bat. *Naturwissenschaften* 69: 192.
- JOSHI, D. & M.K. CHANDRASHEKARAN (1984): Bright light flashes of 0.5 msec reset the circadian clock of a microchiropteran bat. *J. Exp. Zool.* 230: 325-328.
- JOSHI, D. & M.K. CHANDRASHEKARAN (1985): Spectral sensitivity of the photoreceptors responsible for phase shifting the circadian rhythm of activity in a bat. *J. Comp. Physiol. A* 156: 189-198.
- MARIMUTHU, G., S. RAJAN & M.K. CHANDRASHEKARAN (1981): Social entrainment of the circadian rhythm in the flight activity of the microchiropteran bat, *Hipposideros speoris*. *Behav. Ecol. Sociobiol.* 8: 147-150.
- MARIMUTHU, G., R. SUBBARAJ & M.K. CHANDRASHEKARAN (1978): Social synchronization of the activity rhythm in a cave-dwelling insectivorous bat. *Naturwissenschaften* 65: 600.
- NAVANEETHAKANNAN, K. & P. KUMARASAMY (1986): Absence of extraretinal photic entrainment in a diurnal squirrel *Funambulus palmarum* and a nocturnal mouse *Mus booduga*. *Indian J. Exp. Biol.* 24: 730-731.
- NEUWEILER, G. (1984): Foraging, echolocation, and audition in bats. *Naturwissenschaften* 71: 446-455.
- NEUWEILER, G. (1990): Auditory adaptations for prey capture in echolocating bats. *Physiol. Rev.* 70: 615-641.
- NEUWEILER, G., A. LINK., G. MARIMUTHU & R. RÜBSAMEN (1988): Detection of prey in echo-cluttering environments. In: Animal Sonar Processes and Performances [Eds: Nachtigal, P.E. & P.W.B Moore (NATO Series)], New York, Plenum Press. Series A: Life Sciences: 156: 613-616.
- NEUWEILER, G., SATPAL SINGH & K. SRIPATHI (1984): Audiograms of South Indian bat community. *J. Comp. Physiol. A* 154: 133-142.
- RADHAMANI, T.R., G. MARIMUTHU & M.K. CHANDRASHEKARAN (1990): Relationship between size and carrying infants by hipposiderid mother bats. *Curr. Sci.* 59: 602-603.
- SRIPATHI, K. (1982): Light relations of the circadian rhythm in the tropical bat *Taphozous nudiventris kachhensis* Dobson 1872 under semi-natural and laboratory conditions. Ph.D. thesis, Madurai Kamaraj University, Madurai.
- SUBBARAJ, R. & M.K. CHANDRASHEKARAN (1978): Pulses of darkness shift the phases of a circadian rhythm in an insectivorous bat. *J. Comp. Physiol. A* 127: 239-243.
- USMAN, K., J. HABERSETZER., R. GOPALAKRISHNASWAMY & K. PARAMANANDAM (1980): Behaviour of bats during a lunar eclipse. *Behav. Ecol. Sociobiol.* 7: 79-81.

#### 4. THE MALABAR SPINY DORMOUSE *PLATACANTHOMYS LASIURUS* IN MUDUMALAI WILDLIFE SANCTUARY, TAMIL NADU

The Malabar spiny dormouse *Platacanthomys lasiurus* has been reported by Prabhakar (1997) in the Indira Gandhi Wildlife Sanctuary, Tamil Nadu at 650 m; Ganesh (1997) in the Kalakad Mundanthurai Tiger Reserve, Tamil Nadu at 1,100 m; Sankar (1996) in Upper Bhavani Hills at 2,000 m and also by Jayson and Christopher (1995) in Peppara Wildlife Sanctuary, Kerala at 600 m elevation.

The Mudumalai Wildlife Sanctuary is situated in Nilgiri district, Tamil Nadu (11° 32'-11° 43' N; 76° 22'-76° 45' E), with an altitude range of 350-1,266 m above msl. It bears vegetation types varying from Moist Deciduous and Semi-evergreen in the Benne forest, through Dry Deciduous Forest over most of the Sanctuary to Dry Thorn in Moyar.

The ecology and distribution of small